

THE CAMBIUM AND ITS DERIVATIVE TISSUES  
NO. VIII. STRUCTURE, DISTRIBUTION, AND DIAGNOSTIC  
SIGNIFICANCE OF VESTURED PITS IN DICOTYLEDONS

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*With four text figures and plates 61-63*

INTRODUCTION

IN CONNECTION with an extended investigation of plasmodesma, I have had occasion to examine the cell walls and the pit membranes of a wide range of Gymnosperms and Angiosperms. It is evident that many of the structures in the tissues of the higher plants which are hypothesized as evidence for the existence of protoplasmic connections can not be interpreted as such.

The bordered pits in the vessels of the Leguminosæ and of certain other families of Dicotyledons are referred to as "sievelike" or "cribriform," a nomenclature based upon the assumption that the pit membranes are perforated by numerous small openings through which protoplasmic connections occurred in the immature vessel members. The sievelike appearance described by Dutailly (1), Jönsson (4), and others is not due to perforations of the pit membrane, but, as will be shown on the following pages, to minute outgrowths from the free surface of the secondary walls.

Although the so-called cribriform pits of tracheary tissue lose much of their putative physiological significance, they appear to be of considerable value both in the systematic study of woods and in discussions concerning the relationships and classification of specific groups of Dicotyledons.

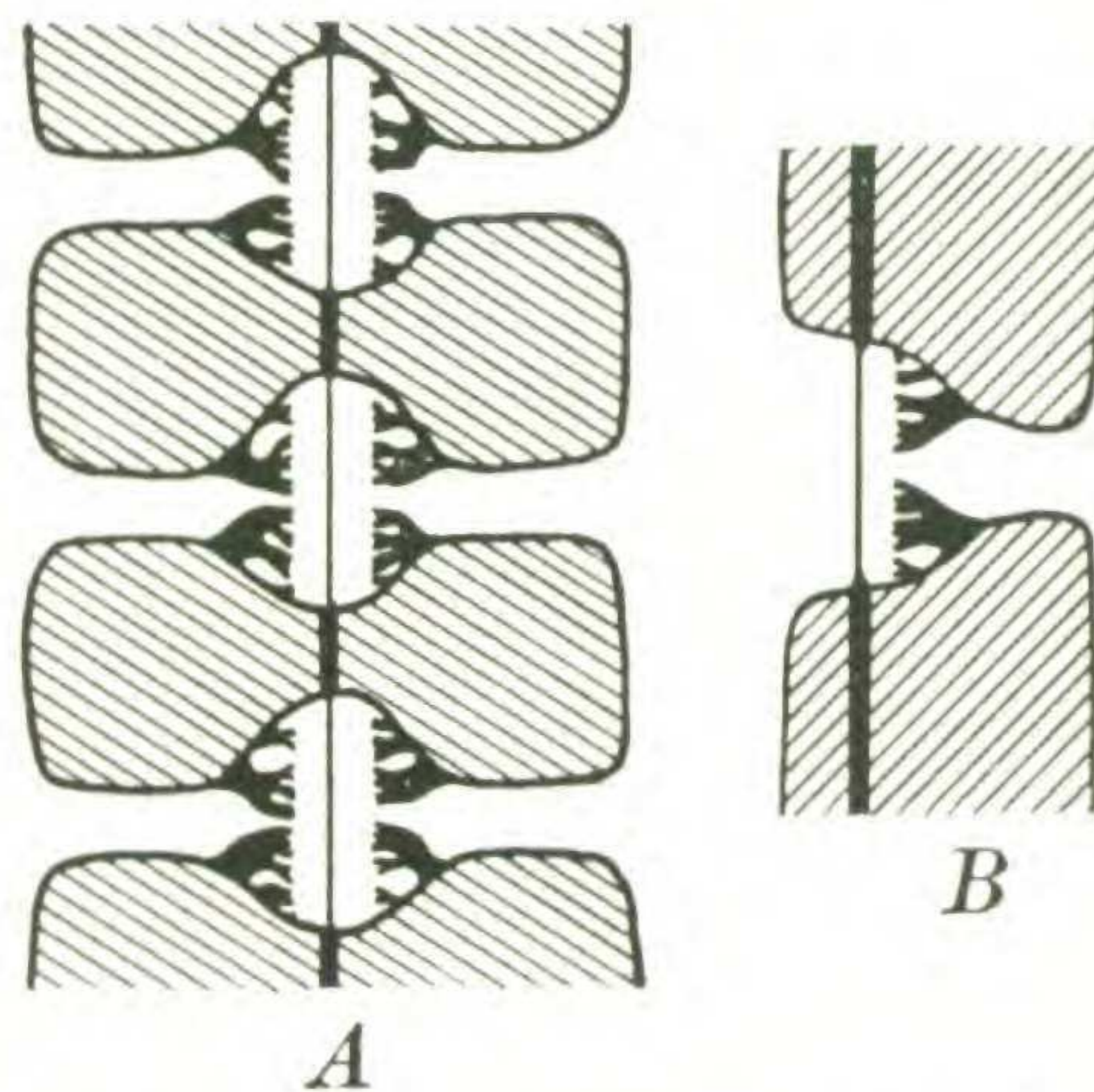
STRUCTURE OF VESTURED (CRIBRIFORM) PITS

In unstained longitudinal sections of the wood of the Leguminosæ, Myrtaceæ, Polygonaceæ, Lythraceæ, Combretaceæ, and of a number of other representatives of the Dicotyledons, the bordered pits have, in surface view, a punctate appearance due to the presence of refractive processes of varying forms. In sections treated differentially with Haidenhain's hæmatoxylin and safranin, these processes are deeply stained and, in photomicrographs, appear as dark spots (*Plate 61, figs. 1, 3, 5, and 7*) or as reticulate structures (*Figs. 2, 4, and 6*) on a lighter colored background. By carefully focusing at successive levels it is



possible to demonstrate that there are two entirely independent sets of deeply-staining processes in each bordered pit-pair and that the punctate appearance of the bordered pits in surface view is not due to an unevenly thickened or perforated pit membrane.

Owing to the small size of the pits and to the thickness of the walls in the tracheary elements of most Dicotyledons, the internal structural details of bordered and half-bordered pit-pairs may be observed most accurately in sectional rather than in surface views. It should be emphasized in this connection, however, that for this purpose extremely thin sections, 5-7 microns, are essential. The pits illustrated in *Plate 61, fig. 7* are shown in section in *Plate 62, fig. 10*. The thick, imperforate pit-membranes are in the median position, and the pit apertures and pit chambers are clearly visible. The dark-colored, toothlike processes obviously are attached to the overarching walls of the pit chambers and are not connected with the pit membranes. The more massive papillæ

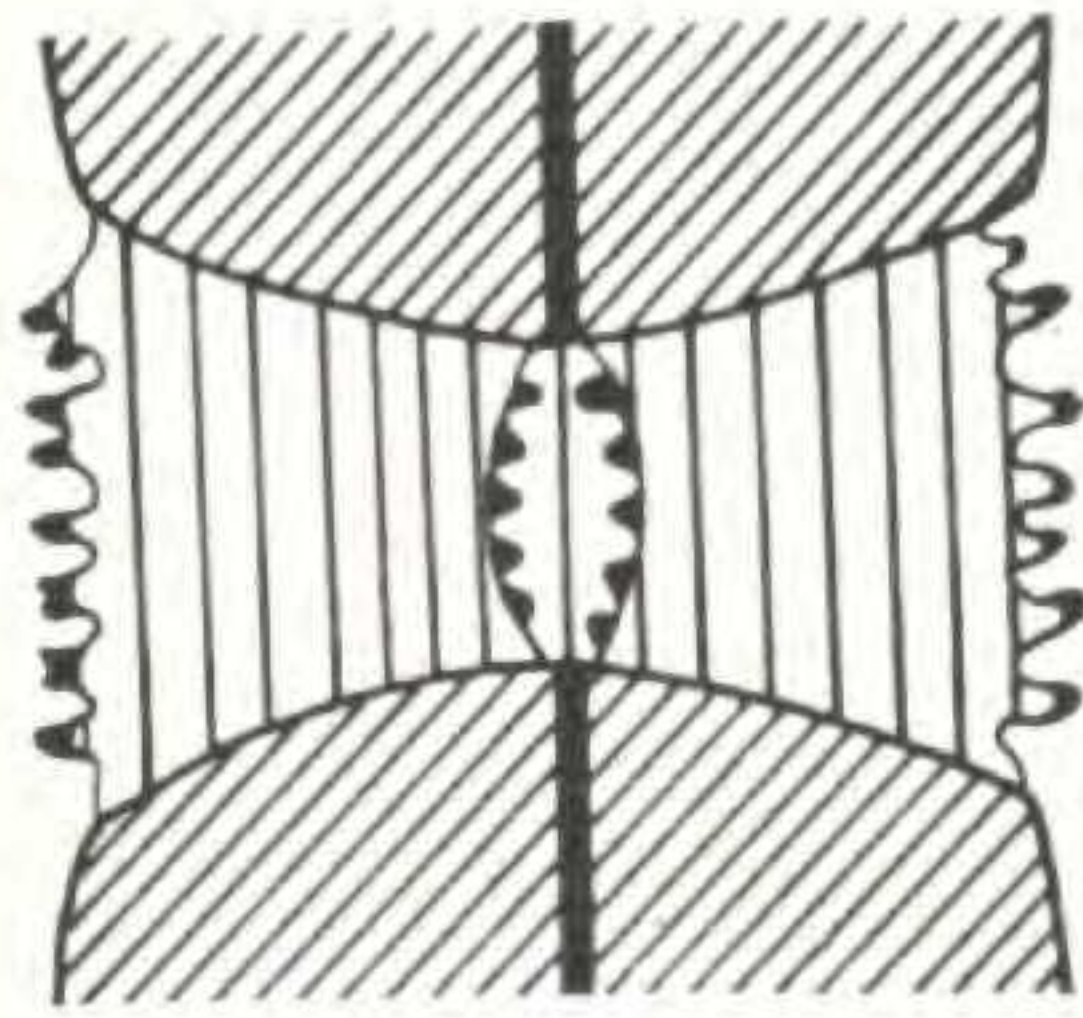


TEXT FIGURE 1. COMBRETUM SPECIES. (A) Sectional view of bordered pit-pairs in the walls of adjacent vessels, showing coralloid outgrowths from the overarching walls of the pit-chambers. (B) Sectional view of half-bordered pit-pair in the adjacent walls of a vessel (right) and of a parenchymatous element (left). The bordered pit is vested, but the simple pit is not.

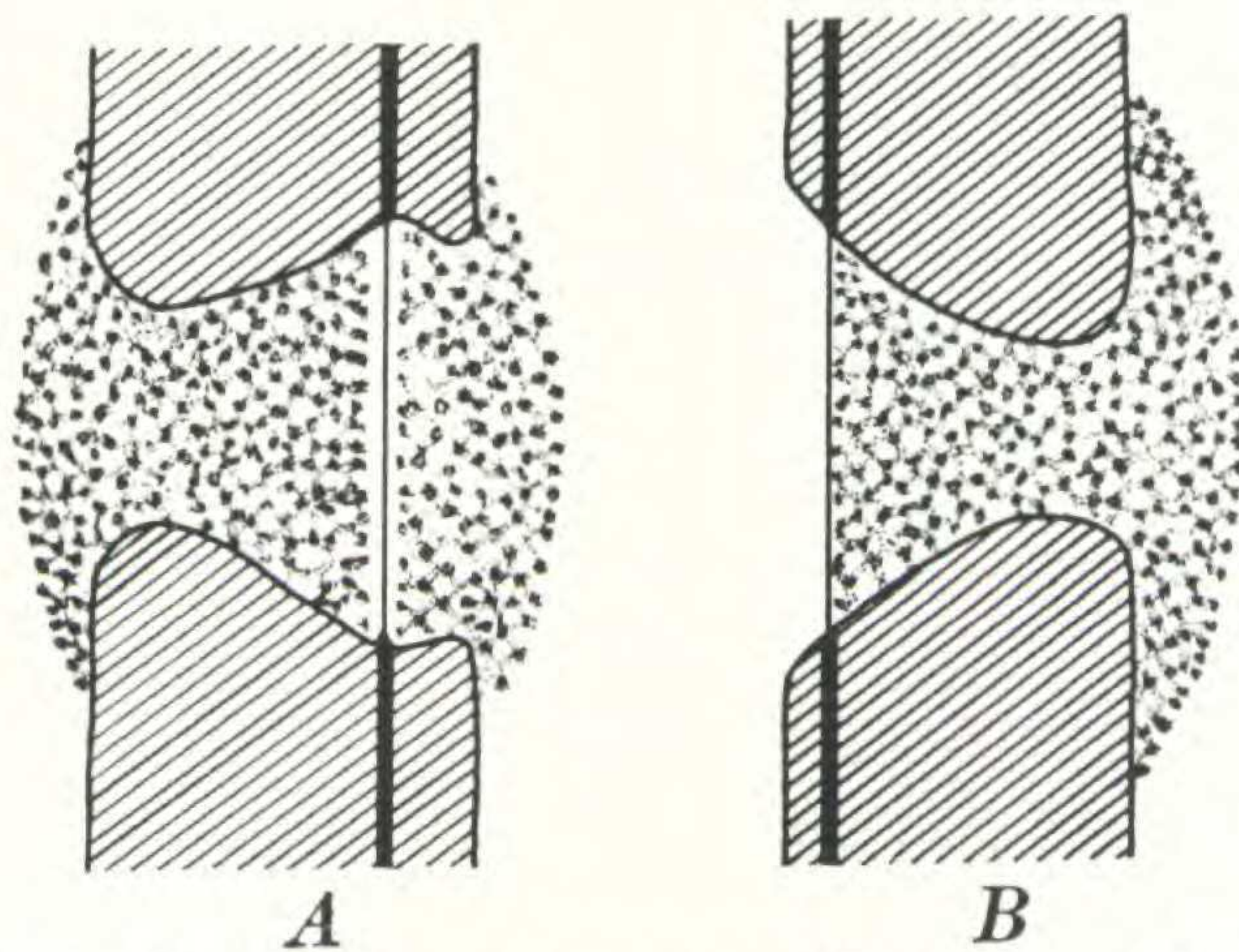
are attached close to the margins of the pit apertures and project diagonally towards the center of the pit chambers. Thus, in *Plate 61, fig. 7*, they are visible through the pit apertures, whereas the smaller peripheral papillæ, on the contrary, are partly obscured by the intervening portion of the secondary wall. *Plate 62, fig. 8* and *Text fig. 1A* are sections through the bordered pits illustrated in *Plate 61, fig. 5*. In these pits, as in the preceding ones, the deeply-stained processes are attached to the overarching walls and project into the pit chambers. They are characterized by having a distinctly branched or coralloid



structure, however. The pit membranes are shown in the median position in *Text fig. 1*, whereas in *Plate 62, fig. 8* they are ruffled and deflected to the right or left. A somewhat different type of structure is shown in *Plate 62, fig. 11*, a section through the bordered pits illustrated in *Plate 61, fig. 4*. Here the dark-colored processes form loose mats of branching and anastomosing filaments which are attached to the over-arching walls of the pit chambers. Denser mats of finer texture which occlude the pit chambers are illustrated in *Plate 61, fig. 2* and *Plate 63, fig. 17*.



TEXT FIGURE 2. *EUGENIA DICHOTOMA* DC. Sectional view of bordered pit-pair in the walls of adjacent fiber-tracheids, showing papillary projections from the margins of both the inner and the outer apertures.

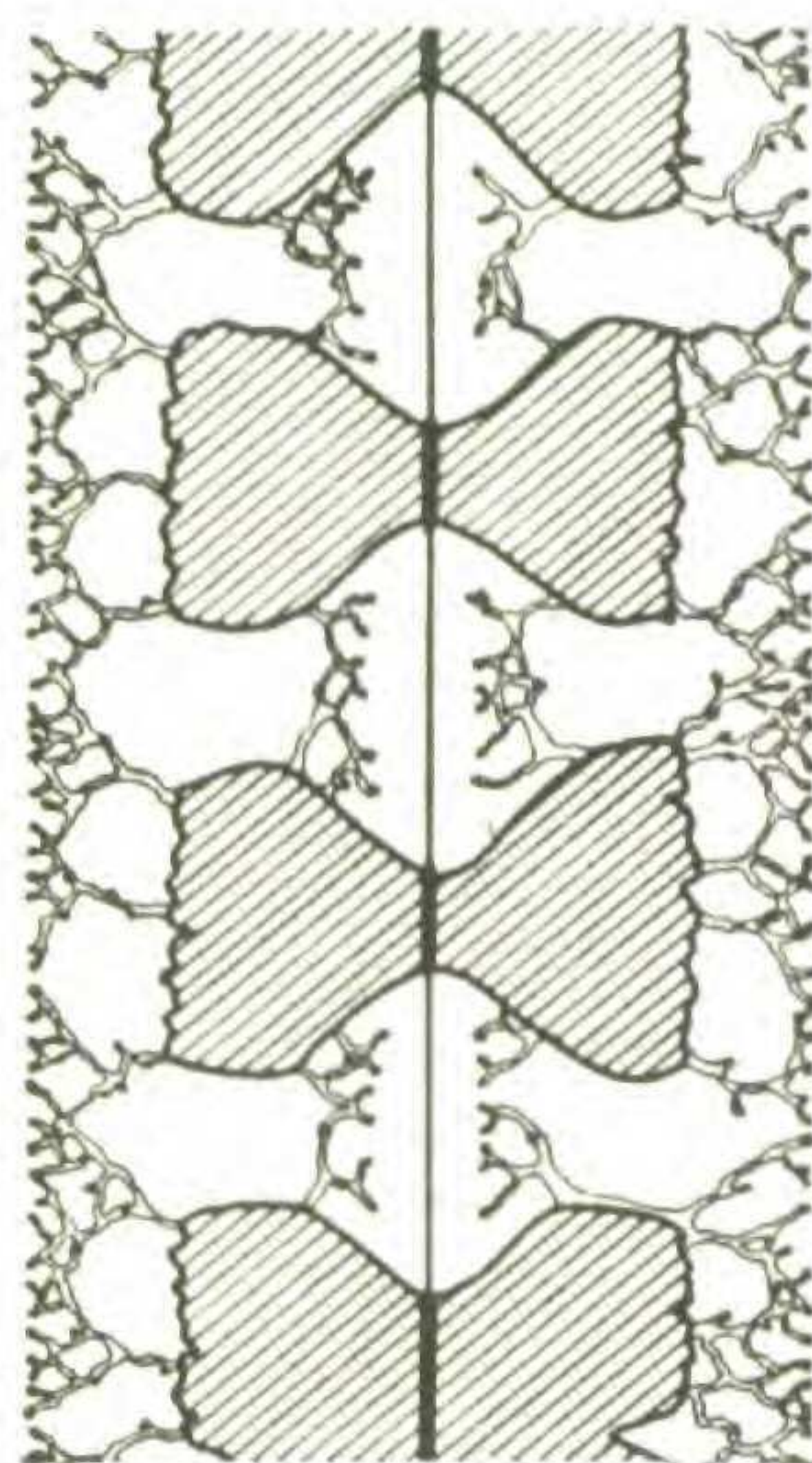


TEXT FIGURE 3. *PARASHOREA PLICATA* Brandis. (A) Sectional view of bordered pit-pair in the adjacent walls of a vessel (left) and of a short tracheid (right). Mats of fine texture fill the entire pit-cavities and project more or less into the lumens of the cells. (B) Sectional view of half-bordered pit-pair in the adjacent walls of a vessel (right) and of a parenchymatous element (left). The bordered pit is vestured, but the simple pit is not.

The papillary, coralloid or filamentous processes are not confined to the pit chambers in all cases. As shown in *Plate 62, fig. 12* and *Text fig. 2*, they may be attached to the margins of both the inner and the outer apertures. They may fill the entire pit cavities and project more



or less into the lumens of the cells (*Plate 62, fig. 9* and *Text fig. 3A*). Not infrequently they occur on the inner surface of the secondary walls of the vessels (*Text fig. 4* and *Plate 63, fig. 16*) as well as within the bordered pits. They appear to be confined to tracheary elements, however. Thus, in half-bordered pit-pairs, they are present in the bordered pits of the tracheary elements but are absent in the simple pits of the adjoining parenchymatous cells (*Plate 62, fig. 13* and *Plate 63, fig. 18, Text figs. 1B* and *3B*).



TEXT FIGURE 4. *VOCHYSIA HONDURENSIS* Sprague. Sectional view of bordered pit-pairs in the walls of adjacent vessels, showing branched and anastomosing projections from the overarching walls of the pit-chambers and from the inner surfaces of the vessels.

In view of such facts as these, the terms *sievelike* or *cribriform* obviously should not be used in discussing the structures originally described by Dutailly and Jönsson. The terms *vestured pits* and *vestured walls* have been substituted for them by the Nomenclature Committee of the International Association of Wood Anatomists.

#### DEVELOPMENT OF VESTURED PITS

*A priori*, the structure of vestured pits and of vestured walls might be interpreted as due to adhering extraneous material deposited in mature tracheary cells during post mortem changes in the drying of sapwood or during the transformation of sapwood into heartwood. A study of living cells in sections of differentiating xylem reveals the fact that the curious processes in reality are formed by the cytoplasm during the later stages of the development of tracheary elements.

It should be noted in this connection, however, that punctate appearances (*Plate 63, fig. 15*) may be produced at times by extraneous or coagulated material which accumulates in the bordered pits during post



mortem changes and particularly during the transformation of sapwood into heartwood. True vestured pits may be distinguished from such artifacts by constancy of form and distribution, as well as by differential solubilities and other tests. In all the plants examined by me the vestured intervacular pits, when present in a species, occur in all vessels throughout a given specimen, in specimens from different parts of a tree, and in material from widely separated sources. The artifacts, on the contrary, are of extremely irregular and sporadic occurrence, not only in different specimens of a particular species, but even within the limits of a single section.

#### DISTRIBUTION OF VESTURED PITS IN DICOTYLEDONS

According to Record (6), pits with so-called cribriform membranes have been reported by Jönssen (4), Heiden (2), Ursprung (7), Moll and Janssonius (5), and Record as occurring in the secondary xylem of 20 families of Dicotyledons. In most cases, the number of species and genera listed is so restricted that it is not possible to formulate reliable conclusions concerning the occurrence and diagnostic value of vestured pits in specific groups of Dicotyledons. In 11 of the 20 families, the character is recorded in a single species or genus.

It seems advisable, accordingly, to tabulate my observations upon 2660 species, 979 genera, 152 families, and 33 orders. Families with vestured pits are printed in italics in Table 1. The numbers of genera and species investigated in each family are recorded in the columns at the right. Families in which "cribriform pits" have been reported by other investigators are marked with an asterisk.

TABLE I.

Orders and Families	Number of genera studied	Number of species studied
VERTICILLATAE		
<i>Casuarinaceæ</i>	1	8
PIPERALES		
<i>Piperaceæ</i>	2	3
<i>Chloranthaceæ</i>	1	1
SALICALES		
<i>Salicaceæ</i>	2	33
GARRYALES		
<i>Garryaceæ</i>	1	1
MYRICALES		
<i>Myricaceæ</i>	2	7



TABLE I. (Continued)

Orders and Families	Number of genera studied	Number of species studied
LEITNERIALES		
Leitneriaceæ	1	1
JUGLANDALES		
Juglandaceæ	5	24
FAGALES		
Betulaceæ	5	48
Fagaceæ*	7	107
URTICALES		
Ulmaceæ	6	33
Moraceæ	15	52
Urticaceæ	10	27
PROTEALES		
Proteaceæ	26	135
SANTALALES		
Santalaceæ	2	5
Olacaceæ	5	6
Octoknemataceæ	1	1
Loranthaceæ	2	2
ARISTOLOCHIALES		
Aristolochiaceæ	1	1
POLYGONALES		
<i>Polygonaceæ</i> *	8	48
CENTROSPERMAE		
Chenopodiaceæ	5	8
Amarantaceæ	1	1
Nyctaginaceæ	2	6
Aizoaceæ	1	1
Caryophyllaceæ	1	1
RANALES		
Trochodendraceæ	3	4
Himantandraceæ	1	1
Cercidiphyllaceæ	1	1
Ranunculaceæ	4	4
Lardizabalaceæ	1	1
Berberidaceæ	1	3
Menispermaceæ	1	1
Magnoliaceæ	10	33
Annonaceæ	16	31



TABLE I. (Continued)

Orders and Families	Number of genera studied	Number of species studied
Myristicaceæ	4	6
Monimiaceæ	3	3
Lauraceæ*	19	47
Hernandiaceæ*	4	6
RHOEADALES		
Papaveraceæ	3	4
<i>Capparidaceæ</i>	8	28
<i>Cruciferae</i>	3	4
Moringaceæ	1	2
ROSALES		
Saxifragaceæ	7	9
Pittosporaceæ	3	17
Brunelliaceæ	1	1
Cunoniaceæ	3	6
Hamamelidaceæ*	8	9
Eucommiaceæ	1	1
Platanaceæ	1	4
Crossosomataceæ	1	1
Rosaceæ*	24	77
Connaraceæ	4	8
<i>Leguminosae</i> *	91	198
Bauhinieæ	2	19
GERANIALES		
Oxalidaceæ	1	1
Linaceæ	1	1
Humiriaceæ	2	2
Erythroxylaceæ	1	4
Zygophyllaceæ	3	7
Rutaceæ	22	46
Simarubaceæ	9	16
Burseraceæ	7	15
Meliaceæ	18	56
<i>Malpighiaceæ</i>	13	33
<i>Vochysiaceæ</i> *	3	12
Trigoniaceæ	1	5
Polygalaceæ	4	4
Dichapetalaceæ	1	1
Euphorbiaceæ*	35	55
<i>Brideliæ</i>	2	6



TABLE I. (Continued)

Orders and Families	Number of genera studied	Number of species studied
SAPINDALES		
Buxaceæ	1	4
Coriariaceæ	1	1
Anacardiaceæ	20	61
Cyrillaceæ	2	2
Aquifoliaceæ	3	12
Celastraceæ	23	53
Salvadoraceæ	1	1
Staphyleaceæ	2	4
Icacinaceæ	6	7
Aceraceæ	1	25
Hippocastanaceæ*	1	6
Sapindaceæ	26	48
Sabiaceæ	2	3
RHAMNALES		
Rhamnaceæ*	9	24
Vitaceæ	3	7
MALVALES		
Elaeocarpaceæ	4	15
Tiliaceæ	12	24
Malvaceæ	9	11
Bombacaceæ	5	8
Sterculiaceæ	9	31
Scytopetalaceæ	1	1
PARIETALES		
Dilleniaceæ	4	14
Eucryphiaceæ	1	3
<i>Ochnaceæ-Exalbuminosæ</i>	5	21
Albuminosæ	2	4
Caryocaraceæ	1	1
Marcgraviaceæ	1	2
Theaceæ	8	11
Guttiferæ*	17	25
<i>Dipterocarpaceæ</i>	8	32
Fouquieriaceæ	1	1
Cistaceæ	1	1
Winteranaceæ	1	1
Violaceæ	4	5



TABLE I. (Continued)

Orders and Families	Number of genera studied	Number of species studied
Flacourtiaceæ	15	31
Stachyuraceæ	1	1
Passifloraceæ	3	4
OPUNTIALES		
Cactaceæ	2	7
MYRTIFLORAE		
<i>Oliniaceæ</i>	1	2
<i>Thymelæaceæ</i>	3	3
Elæagnaceæ	3	6
<i>Lythraceæ</i> *	3	10
<i>Sonneratiaceæ</i> *	1	2
<i>Blattiaceæ</i> *	1	2
<i>Crypteroniaceæ</i> *	1	2
<i>Punicaceæ</i>	1	1
Lecythidaceæ	18	45
Rhizophoraceæ	13	32
Nyssaceæ	1	4
Alangiaceæ	1	1
<i>Combretaceæ</i> *	7	24
<i>Myrtaceæ</i> *	15	89
<i>Melastomataceæ</i> *	4	9
<i>Oenotheraceæ</i> *	1	3
UMBELLIFLORAE		
<i>Araliaceæ</i> *	25	66
Umbelliferæ	2	2
<i>Cornaceæ</i> *	7	15
ERICALES		
Clethraceæ	1	3
Ericaceæ	8	24
Epacridaceæ	3	9
PRIMULALES		
Myrsinaceæ	8	19
EBENALES		
Sapotaceæ	11	49
Ebenaceæ	2	27
Symplocaceæ	2	6
Styracaceæ	4	8



TABLE I. (Continued)

Orders and Families	Number of genera studied	Number of species studied
CONTORTAE		
Oleaceæ*	16	59
<i>Nathusia</i>	1	1
<i>Forestiera</i>	1	5
<i>Loganiaceæ</i>	6	7
<i>Apocynaceæ</i>	15	29
<i>Asclepiadaceæ</i> *	1	2
TUBIFLORAE		
Convolvulaceæ	1	2
Polemoniaceæ	1	2
Hydrophyllaceæ	1	1
Boraginaceæ	5	19
Verbenaceæ	12	29
Labiataë	4	6
Solanaceæ	6	11
Scrophulariaceæ*	6	9
Bignoniaceæ	11	25
Gesneriaceæ	1	1
Myoporaceæ	2	3
RUBIALES		
<i>Rubiaceæ</i> *	41	78
Caprifoliaceæ*	5	18
Dipsacaceæ	2	2
CUCURBITALES		
Cucurbitaceæ	1	2
CAMPANULATAE		
Compositæ*	12	21

## DIAGNOSTIC VALUE OF VESTURED PITS

In the material examined by me, true vestured pits are either present throughout the secondary xylem of a species or genus or are entirely absent. A similar constancy in the presence or absence of these structures appears to prevail in most families of Dicotyledons. In only four of the 152 families tabulated in Table 1, have I encountered vestured pits in certain representatives of a family and not in others. It should be noted in this connection, however, that in three of the four families the distribution of vestured pits correlates with major subdivisions. Thus, in the Leguminosæ, the vestured pits are present in all the species



and genera examined, with the exception of the Bauhinieæ, whereas in the Euphorbiaceæ they are absent except in the Brideliæ. They are present in the Exalbuminosæ of the Ochnaceæ, but appear to be absent in the Albuminosæ. In other words, the Oleaceæ, are the only family in which the distribution of vestured pits fails to correlate closely with the systematic classification.

It may be objected that cribriform structures have been reported in representatives of 13 families which are not italicized by me. These families are listed in Table 2.

TABLE 2

Families	Genera and species	Reported by
Fagaceæ	<i>Quercus alba</i> L.	Jönsson (4)
	<i>Q. Cerris</i> L.	"
	<i>Q. pedunculata</i> Ehrh.	"
	<i>Q. obtusiloba</i> Michx.	"
Lauraceæ	Numerous genera and species	Janssonius (3)
Hernandiaceæ	<i>Hernandia peltata</i> Meisn.	"
Hamamelidaceæ	<i>Altingia excelsa</i> Nor.	Moll & Janssonius (5)
Rosaceæ	<i>Cerasus serotinus</i> hort.	Jönsson (4)
	<i>Prunus brigantiaca</i> Vill.	"
Hippocastanaceæ	<i>Aesculus Hippocastanum</i> L.	"
	<i>A. rubicunda</i> hort.	"
Rhamnaceæ	<i>Phyllica ericoides</i> L.	"
Guttiferæ	<i>Calophyllum Inophyllum</i> L.'	Ursprung (7)
	<i>C. Calaba</i> Jacq.	Record (6)
Araliaceæ	<i>Hedera helix</i> L.	Jönsson (4)
Cornaceæ	<i>Mastixia trichomata</i> Blume	Moll & Janssonius (5)
Scrophulariaceæ	<i>Veronica Andersoni</i> hort.	Jönsson (4)
Caprifoliaceæ	<i>Viburnum sundaicum</i> Miq.	Janssonius (3)
Compositæ	<i>Helichrysum moniliferum</i> hort.	"

Obviously it is essential to determine whether the "sieve-like" appearances reported by Jönsson and others are due to the presence of vestured pits or to artifacts such as are produced during post mortem changes or during the transformation of sapwood into heartwood.

As indicated in Table 1, true vestured pits do not occur in any of the 107 species of Fagaceæ that I have studied. Nor have I succeeded



in finding them in any of the numerous specimens of *Quercus alba*, *Q. Cerris*, *Q. obtusiloba*, or *Q. robur* L. (*Q. pedunculata* Ehrh.) that I have investigated. Not only are vestured pits entirely absent in 19 genera and 47 species of the Lauraceæ and in 77 species and 24 genera of the Rosaceæ, but also in numerous specimens of the Prunoideæ, i. e., *Prunus* and its subgenera *Prunophora*, *Amygdalus*, *Cerasus*, and *Padus*. Similarly, I have been unable to find vestured pits in *Altingia*, the Bucklandiæ, Altingiæ, Parrotiæ, and Hamamelideæ of the Hamamelidaceæ; in *Aesculus Hippocastanum*, and five other species of the Hippocastanaceæ; in the Zizypheæ and Rhamneæ of the Rhamnaceæ; in *Calophyllum Inophyllum* and other Calophylloideæ of the Guttiferæ; in *Hedera helix* and 65 other representatives of the subgroups, Schefflereæ and Aralieæ, of the Araliaceæ; or in the Mastixioideæ and Cornioideæ of the Cornaceæ.

Although I have failed to find true vestured pits in any of the families listed in Table 2, I have frequently encountered artifacts of various types. In such genera as *Quercus*, *Altingia*, *Calophyllum*, *Hedera*, *Mastixia*, etc., these artifacts may produce a punctate appearance which closely simulates that of vestured pits. Therefore, in view of the fact that punctate appearances were interpreted as evidence of a sievelike structure, it is not surprising that the species in Table 2 were recorded as having pits with cribriform membranes.

It should not be inferred from this that more detailed and extensive surveys may not reveal the presence of vestured pits in additional families of Dicotyledons. The vestured condition appears to have arisen independently a number of times. To assume that all plants with vestured pits are closely related or are derived from common ancestors which possessed such structures leads to a *reductio ad absurdum*. Vestured pits occur in the more highly specialized types of tracheary tissue and are absent in plants which have a primitive combination of structural characters in the xylem. If vestured pits have arisen independently a number of times, it is not unlikely that genera may ultimately be found in which these structures are present in certain species and are absent in others. It may be inferred, however, from a statistical analysis of Table 1, that sporadic distributions of vestured pits are likely to be of relatively infrequent occurrence in the case of subgenera, genera, and subfamilies.

That vestured pits are extremely useful diagnostic criteria in the systematic study of woods was clearly demonstrated during the course of the present investigation. Most collections of wood specimens, even when accompanied by herbarium specimens, contain a varying number of errors. In other words, the fact that an herbarium specimen and a



sample of wood bear the same number is unfortunately no guarantee that both specimens came from the same tree or that the herbarium specimen was correctly identified. Collections of woods commonly pass through a number of hands and may be subdivided, renumbered, or relabeled. Furthermore, transpositions are likely to occur during the preparation of microscopic slides unless a painstaking system of checking and rechecking is employed. In my reconnaissance of Dicotyledons, I encountered true vestured pits in slides of putative representatives of a number of families which are not italicized in Table 1, and, conversely, ordinary bordered pits in families which are italicized. In all these families, with the exception of the Oleaceæ, the aberrant specimens proved to be errors which could thus be eliminated from the collections.

Similar combinations of anatomical characters occur not infrequently in the woods of families which are widely separated in the systematic classification of Dicotyledons. For example, the secondary xylem of the Osage Orange, *Maclura pomifera* (Raf.) Schneid., so closely resembles that of the Black Locust, *Robinia pseudoacacia* L., that it is extremely difficult to distinguish the woods by anatomical criteria. The woods of the two genera may be identified with certainty, however, by the fact that vestured pits occur in *Robinia* and are entirely absent in *Maclura*.

As indicated in the accompanying text figures and photomicrographs, the number, size, and form of the refractive processes vary considerably in different plants. In certain species and genera the processes are confined to the intervacular pits, whereas in others they may occur as well in the half-bordered pit-pairs, in the fiber tracheids, or upon the inner surfaces of the tracheary walls. Such differences may obviously be utilized as diagnostic criteria in the systematic study and classification of woods.

#### SUMMARY AND CONCLUSIONS

1. Many of the structures in the tissues of the higher plants which are hypothesized as evidence for the existence of protoplasmic connections can not be interpreted as such.
2. The so-called sievelike appearance of the pits in the vessels of Leguminosæ and of other families of Dicotyledons is not due to perforations of the pit membranes, but to minute outgrowths from the free surfaces of the secondary walls.
3. These refractive processes which vary considerably in size, number, and form are not confined to the pit-chambers in all cases, but may occur on the inner surface of the secondary walls of the vessels.



4. They appear to be restricted to tracheary elements; in half-bordered pit-pairs they are present in the bordered pits of the tracheary elements, but are absent in the simple pits of the adjoining parenchymatous cells.
5. Pits which have these refractive processes may be referred to as *vestured*.
6. In the Dicotyledons (2660 species and 979 genera) examined by me, vestured pits are either present throughout the secondary xylem of a species or genus or are entirely absent. A similar constancy in the presence or absence of these structures appears to prevail in most subfamilies and families.
7. Vestured pits, therefore, are of considerable value both in the systematic study of woods and in discussions concerning the relationships and classification of specific groups of Dicotyledons.

#### ACKNOWLEDGMENTS

The text-figures used in this paper were drawn by my assistant, Mrs. Ernest C. Abbe. I am much indebted to Professor S. J. Record for his kindness in providing woods of various families of Dicotyledons.

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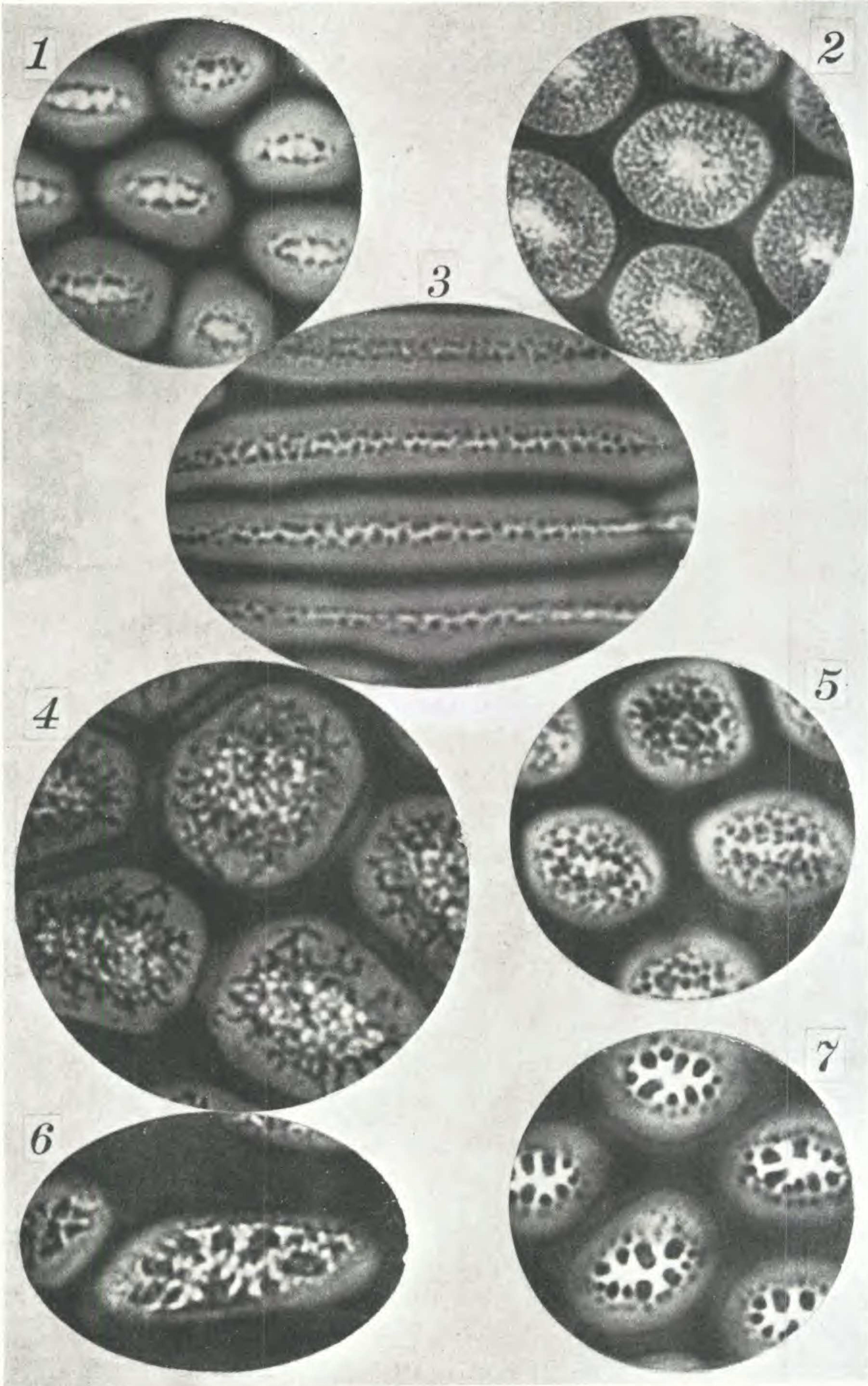
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#### DESCRIPTION OF PLATES

##### PLATE 61

- Fig. 1. *Prosopis juliflora* DC. Surface view of bordered pits, showing toothed appearance of pit apertures.  $\times 2500$ .
- Fig. 2. *Duabanga moluccana* Blume. Surface view of bordered pits, showing finely punctate appearance.  $\times 1900$ .
- Fig. 3. *Fuchsia Colensoi* Hook. f. Surface view of bordered pits, showing toothed appearance of elongated pit apertures.  $\times 2500$ .
- Fig. 4. *Tibouchina mutabilis* Cogn. Surface view of bordered pits, showing mats of branching and anastomosing processes.  $\times 2500$ .
- Fig. 5. *Combretum species*. Surface view of bordered pits, showing coarsely punctate appearance.  $\times 2500$ .





VESTURED PITS IN DICOTYLEDONS